BROOD CHRONOLOGY OF THE COMMON RAVEN

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The Common Raven (*Corvus corax*) is a widely distributed Holarctic species (Goodwin 1976). This corvid occurs over most of the western United States (Good 1952), but is common only in restricted, often remote locations (Bent 1962).

Aside from the descriptions of nest construction by Kulczycki (1973), behavior of captive ravens (e.g., Gwinner 1965), and the observational reports by Kochert et al. (1976, 1977), few investigations have been published that describe the nesting chronology and reproductive biology of a large population of free-flying ravens. The study reported herein was undertaken as a part of a larger investigation (Stiehl 1978) and describes the nesting chronology and reproductive success of a population of Common Ravens in southeastern Oregon.

STUDY AREA AND METHODS

Field work was conducted near Malheur National Wildlife Refuge, located in Harney County, Oregon. This large area (73,250 ha) has an average elevation of 1350 m. The major land forms consist of alkaline lake and marshland covering 32,400 ha, river valley uplands supporting *Carex* and other submerged and emergent plants, and extensive rimrock areas of volcanic and fault block origin. On the plateaus of the surrounding area above the rimrocks, typical Great Basin desert vegetation of sagebrush (*Artemesia* sp.) and greasewood (*Sarcobatus* sp.) form the dominant communities. The extensive rimrock formations provide locations for nest-sites and the vast wetland provides a food base for a nesting population of 40–50 pairs of ravens.

In 1975, potential nest-sites were located by systematically searching rimrocks, suitable trees, and deserted buildings during the nesting season. As a nest was found, the location was plotted on a map and the site marked with plastic flagging. In 1976 and 1977, each nest was inspected at least once within each 7-day period throughout the nesting season. I used an auto mirror attached to a 1.5-m length of soft copper tubing similar to that used by Rowley (1973) to inspect nest contents where direct observation was not possible.

RESULTS

Nest location. —During the study I observed a total of 87 active Common Raven nests. Forty-five nests were found in 1976 and 42 nests in 1977. The nest density was $\frac{1}{22}$ km^2 for the 32 nests on the refuge in 1976 and $\frac{1}{25.2}$ km^2 for 29 nests in 1977. The nesting density was lower for nests off the refuge, but could not be calculated accurately as nests were scattered in the patchy habitat. Most nests (74%, N = 64) were situated on rimrocks. Abandoned buildings and windmills accounted for 23% (N = 20) of the nest-sites and three nests were located in trees (western juniper [*Juniperus occidentalis*] and willow [*Salex* sp.]).

Regardless of substrate, 49% (N = 43) of the nests were used for both of the years of study. Refuge personnel stated that several nests had been active for at least 6 years at the same location. No physical conflict for nest-sites was observed during the study, but Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks (*Buteo jamaicensis*) and Golden Eagles (*Aquila chrysaetos*) nested in the same habitats in the area. A nest used by Golden Eagles and another used by Great Horned Owls in 1976 were used by ravens in 1977. Two nests, which ravens used in 1976, were used by Great Horned Owls in 1977. Prior to my study, a nest built by ravens was used by ravens, Red-tailed Hawks, and Great Horned Owls in 3 consecutive years (John Scharff, pers. comm.).

There appeared to be no relationship between the success (fledging of one or more young) of the nesting attempt and the reuse of the same nest the following nesting season. I used differences in aggressive behavior as I approached the nest (Knight 1984), and peculiarities in vocal patterns (Brown 1974) to identify eight nesting pairs of ravens. Of this group, four pairs used the same nest, after some reconstruction and repair, in both 1976 and 1977. Two pairs built a new nest and attempted to renest the same year after nest failure and two pairs changed nest location in 1977 after successfully nesting in 1976.

Nest construction.—Nest construction that I observed (N = 17) resembled that reported by Kulczycki (1973). After a territory was established in late February (Stiehl 1981), both partners participated in nest construction or repair. Sagebrush and greasewood were placed and woven until a large basket (20 cm × 40 cm diameter) lined with cattle hair, shredded juniper bark, and grasses was formed (Fig. 1). I observed both members carrying these materials to the nest site, but only noted the female actually building the basket.

Although the average diameter of 46 nests was 40.5 ± 4.5 cm, this dimension seemed to be related to the type of substrate used. Nests on rimrock ledges usually filled the space available. Nests in buildings and trees were generally larger than rimrock nests.

Normal compacting of the nest by the chicks and adults, and fouling of the nest by the chicks, as well as seasonal deterioration, necessitated reconstruction prior to reuse. Reconstruction was also observed when the same nest was used twice in the same nesting season, after failure of the first clutch (N = 4), even though the nest appeared to be structurally sound. The reconstruction was similar to new construction; however, no new soil was added to the existing structure.

Egg-laying and incubation.—Egg-laying began in early March. Exact dates were established based on visual inspection on at least 2 consecutive

Fig. 1.   A typical rimrock nest of a Common Raven. The nest is about 4 m above the ground.

TABLE 1

NESTING PHENOLOGY FOR *CORVUS CORAX*, MALHEUR NWR, 1976–77

Period	No. of nests with		
	Eggs	Hatchlings	Fledglings
7–15 March	8	0	0
16–31 March	15	4	0
1–15 April	24	16	0
16–30 April	12	20	0
1–15 May	11	10	8
16–31 May	1	8	18
1–15 June	0	2	11
16–31 June	0	0	8
1–7 July	0	0	4
Exact period unknown	0	0	4
Total	71	60	53

days, with at least 1 day when no eggs were present, or calculated on the hatching or fledging dates of birds in a particular nest. Using both of these methods, the median laying date for both years was 4 April and egg-laying occurred from 7 March to 16 May (Table 1). The median includes some known second and third clutches.

In 14 observations of the complete egg-laying sequence, a 24-h delay followed the laying of the first egg. After this, eggs were layed at about 24-h intervals until the clutch was complete. Based on observations of hatching sequence (N = 12), I determined that incubation began with the second egg laid, contrary to the reports of Gwinner (1965) and Goodwin (1976) but in agreement with Holyoak (1967). For the population I studied, the incubation period was 20.9 ± 1.16 days for 36 nests. The mean clutch-size for 19 nests was 5.8 (SD = ±1.1) in 1976 and was 6.1 (SD = ±0.8) for 26 nests in 1977. Ratcliffe (1962) reported a mean clutch-size of 4.6, whereas Holyoak (1967) gives 5.2 as a mean clutch-size. Kochert et al. (1976) reported a mean of 5.2 eggs (N = 10) for ravens nesting in southwestern Idaho in 1976, and 5.38 (N = 21) in the following year (Kochert et al. 1977). Holyoak (1967) suggests that the clutch-size varies from 3 to 6 eggs. Goodwin (1976) also states ravens lay from 3 to 6 eggs, rarely fewer than 3 and very rarely 7 eggs. During this study, the clutch-size of 45 nests could be accurately determined. Fifteen nests (33%) were found with a complete clutch of 7 eggs. The differences in clutch-size may be attributed to more abundant food sources in my study area or perhaps an adaptation to optimum survivorship as suggested by Lack (1954).

I only saw females incubating eggs, but males provided food for females during incubation. I recorded 23 such feedings of two basic types. As the male approached the nest, direct feeding was initiated by quivering (Goodwin 1976) and *"koww"* calls (Brown 1974) by the female. Food was then regurgitated by the male in a manner typical of chick feeding. If the female did not vocalize, the food was placed on the nest rim or within 2 m of the nest by the male. When near the nest, the male would "stand guard" (cf. Bent 1962) in a prominent location with a commanding view of the area, but direct view of the nest did not appear to be critical.

The nest was occasionally unattended when the female left for short (ca. 10 min) periods. The frequency of these flights increased from two per 10-h period early in incubation to five in an 8-h period during the latter stages of incubation. The purpose of these flights was not determined.

Females left the nest to assist their mate in nest defense against other ravens (N = 6), Red-tailed Hawks (N = 2), and Golden Eagles (N = 1). In all cases, the female joined the male after he began his pursuit and she returned before the male returned to the nest.

Hatching.—Normally one of the eggs failed to hatch (cf. Goodwin 1976). Unhatched eggs remained in the nest from 4 to 7 days after the other eggs hatched. The fate of an unhatched egg was not determined in this study, but Holyoak (1967) states that brood parents consume it within 12 days. I analyzed over 1100 regurgitated pellets and found raven egg shell in five. These shells, however, may have been from either hatched or unhatched eggs, or perhaps depredated eggs from other nests.

The average brood-size for 1976 was 4.0 ± 1.6 (N = 25) and for 1977 was 4.4 ± 1.8 (N = 26). Kochert et al. (1976, 1977) reports average brood sizes of 3.66 (N = 21) and 3.09 (N = 22). For nests with both clutch-size and brood numbers known (N = 41), 69% of the eggs hatched in 1976 and 71% hatched in 1977.

I could not elicit chick begging until 3 days post hatch, indicating that audition did not function at hatch, that sound recognition required several days to develop, or that chicks were not physically able to beg at an earlier age. At 6 days post hatch, vocalizations accompanied the begging. Dorsal pterylae were first visible as a grey band at 5–6 days. Eyes opened between 12 and 14 days post hatch. The development of sight accompanied a major behavioral change in the chicks. Between 6 and 14 days post hatch, I could easily elicit begging and vocalizations. After the eyes opened, the 14-day-old chicks crouched low in the nest and remained silent at my approach. If the reaction were similar to potential nest predators, then locating the nest could have been facilitated by the vocalizations of the chicks. As 71% (N = 12) of the nest depredations occurred between hatch

and 14 days post hatch, the development of sight appeared to be critical to nesting success. No predators were observed, but signs at the nests suggested coyote (*Canis latrans*), raccoon (*Procyon lotor*), weasel (*Mustela* sp.), Great Horned Owl, and man. I was often harassed by the adults during nest inspections, but the defense would not have been sufficient to effectively deter most mammalian predators.

Renesting.—Neither the depredation of eggs nor hatchlings necessarily precluded reproductive success of the nesting pair. Six pairs laid replacement clutches following destruction of the eggs or chicks. Additionally, based on normal dates of nesting, two other pairs laid replacement clutches during the study. One pair renested three times in the 1976 season, and another renested after the loss of both the female parent and the brood. The brood was destroyed at about 16 days post hatch. The female had been shot and was found dead near the nest. There was another set of eggs in the nest. The male had remated and, using the same nest, the new pair successfully reared a brood.

The ability to lay replacement clutches has been reported in many species, including some corvids. Took (1937) reported renesting in Carrion Crows (*C. corone*) and Rowley (1973) reported clutch replacement in the Little Raven (*C. mellori*). Bowles and Decker (1930) noted replacement clutches in *C. corax* after egg predation. Laying replacement clutches after loss of chicks has not, to my knowledge, been reported previously for Common Ravens. Nest loss did not always result in another nesting attempt. Although there were six depredations of nests with eggs or chicks after 5 May, I recorded only three renesting attempts after that date. After a nesting failure, nest construction efforts were accelerated and resulted in a period as short as 11 days between loss and completion of a replacement clutch. Initial nesting attempts required 14–20 days, suggesting that some time is required for initial territorial establishment. After nest loss, I observed either reuse of the same nest (N = 4) after some reconstruction, or building and use of a new nest (N = 2) within 100 m of the old nest. The same nesting substrate was used in 5 of the 6 cases.

Fledging.—For 122 nestlings of known age in my population, fledging started at 41 days (±3) post hatch. Higher precision is impossible due to asynchronous hatch. Sustained flight is not possible for young ravens even after fledging. Young forced from the nest at 35–45 days post hatch glide up to 150 m from the nest and then hop back to the nest. Short flights were characterized by very rapid wing beats and an extended recovery period, during which panting was observed and frequent distress calls were heard.

The mean fledging success was 2.2 (SD = ±2.1) for 25 nests in 1976 and 2.5 (SD = ±2.0) for 28 nests in 1977 (Table 2). Kochert et al. (1976)

TABLE 2

NESTING SUCCESS FOR *CORVUS CORAX*, MALHEUR NWR, OREGON, 1976–77

	1976		1977		All years	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
Eggs	19	5.8 ± 1.1	26	6.1 ± 0.8	45	6.0 ± 0.9
Hatch	25	4.0 ± 1.6	26	4.4 ± 1.8	51	4.2 ± 1.7
Fledged	25	2.2 ± 2.1	28	2.5 ± 2.0	53	2.3 ± 2.0

reports similar success for the same period. Of the 85 nesting attempts observed during the study, 51 (60%) were successful in fledging one or more young. Hooper et al. (1975) reported 63% nest success, whereas Allin (1968) reported 80% success. Dorn (1972) reported 58% success. Factors that decreased fledging success in this study included depredation (N = 20 nests), starvation (N = 7 nests), human disturbance (N = 5 nests), and falling from the nesting substrate (N = 2 nests). Considering these losses, 74% (N = 90) of the hatched young subsequently fledged during the study period.

Examination and palpation of 71 dead nestlings indicated that starvation was the probable cause of death for 16 nestlings (22% of total nestling death [N = 71]) in 1976 and 34 (33% of total nestling death [N = 103]) in 1977. The higher percentage in 1977 coincided with a drought which delayed peak waterfowl nesting about 14 days, whereas the raven nesting period was the same for both years. Avian eggs (principally waterfowl) formed a high proportion of the diet for 13 of the 25 nesting pairs in which starvation occurred. This suggests that a delayed waterfowl nesting season may have accounted for the higher starvation rate in 1977, and may reinforce the suggestion that asynchronous hatch is an adaptation to variations in food availability as suggested by Lack (1947) and Lockie (1955).

I noted two different behavior patterns of the fledglings that appeared to be associated with the date of fledging. Due to nest destruction and predation, the fledging period extended from 8 May to 7 July (Table 1). The ravens that fledged early in the season (8 May–25 May) were presumed to be from successful first nesting attempts. All successful renesting attempts I recorded resulted in fledging after 1 June. Therefore if fledging occurred after 1 June, the first nesting attempt was presumed to have failed.

Behavior of young fledged early in the nesting season. — The young that fledged early in the season (before 25 May) were observed in the vicinity

of the nest for up to 6 weeks after they were seen flying for short distances. During this period, although the fledglings became adept at flying, the adults continued to provide food for them. Both adults fed the young. Upon arrival of an adult, all fledglings directed their attention toward that adult, even if the returning bird did not have food. The young hopped or flew to the adults and begged intensively. One to three young were fed by adults upon arrival, although some young were fed more frequently than others. The probability of being fed at a particular time appeared to be related to begging intensity, however, all young were fed at least once during each of my 4-h observation periods ($N = 8$) at five nests. Food was either regurgitated directly into the gaping mouths or placed on the ground near the larger fledglings. Up to 4 or 5 weeks post hatch, the young were never observed more than 200 m from the nest, perched either on the rimrock (rimrock nests), buildings or other structures (structure nests), or nearby trees and shrubs (tree nests). From these sites, the fledglings made short flights which resulted in 10–15-m vertical drops. The flight by the first fledgling to depart was then mimicked by the rest of the brood.

After 4–5 weeks (65–78 days post hatch) the young accompanied the adults on flights, but the nest-site remained the center of activity. Due to the terrain, the purpose and extent of these flights were not determined. Typically both adults accompanied the brood on these flights. I suspect that the main purpose of these flights was feeding, and that such family flights possibly play an important role in the formation of food preferences in the young. Early morning and late evening observations indicated that the nest-site was used as a roost by the family until the group left the area.

Behavior of young fledging late in the nesting season. — Young that fledged late in the season, probably because of failure of an earlier nesting attempt, displayed behaviors similar to those just described, except that the period of "nest-centered" behavior was compressed. The fledglings remained near the nest for only 5–7 days, and followed the adults for short distances (500 m) as early as 50 days post hatch. Observations of young 500–800 m from the nest were not uncommon for the young which fledged late in the season. I observed less "practice" flying, and although the fledglings did not appear to develop flight skills any faster than early fledged young, they attempted to follow the adults at 10–14 days after fledging (47–54 days post hatch).

The differences in the behavior of fledglings appeared to be related to changes in food preference or availability that occurred in July. The diets of ravens shifted from carrion, small mammals, and eggs to insects, principally grasshoppers (Orthoptera), at that time. Although the availability of small mammals (based on trapping success) and carrion was unchanged,

fewer eggs were available. Ravens were noted more often feeding in areas that had large populations of grasshoppers. In response to the change in the diet, family groups spent more time away from the nest-sites, gathered into increasingly larger flocks, and emigrated from the study area. I saw large flocks of ravens feeding on grasshoppers in cultivated fields up to 100 km from the study area in August of both study years.

Hatchling anomalies.—A total of 214 hatchling ravens from 51 nests were recorded in the study. Of these, seven birds (3.3%) from three nests had detectable anomalies. As no tissues were collected for analysis, the cause of these anomalies could not be determined.

Five ravens, all from the same nest, had gross foot deformities that prevented perching and grasping of food. Ravens often hold down their food in one or both feet as it is eaten. The dead young appeared to have died from either exposure (1 case) or starvation (4 cases). Although the starvation was a result of the foot deformities, it was probably facilitated when the adults deserted the young after the first fledgling died.

Two hatchlings, from separate nests, had malformed beaks. Both were found dead near the nest and were estimated to be from 20 to 25 days old. Other siblings did not appear deformed, and as the adults did not appear to alter their feeding patterns, the other young of the broods (three and two birds, respectively) may have benefited, through increased feeding by the adults, from the death of the deformed hatchling.

SUMMARY

Brood chronology and nesting success of the Common Raven (*Corvus corax*) were studied during 1976 and 1977 nesting seasons on Malheur National Wildlife Refuge in southeastern Oregon. Nest construction or reconstruction began in late February and early March. Egg-laying began during the second week of March and continued through early May. Peak egg-laying occurred the first week of April. In 1976 the mean clutch-size was 5.8 eggs/clutch (N = 19) and in 1977 was 6.1 eggs/clutch (N = 26). The incubation period was about 21 days. Hatching success was 4.0 eggs/clutch in 1976 (N = 25) and 4.4 eggs/clutch in 1977 (N = 26). Productivity was 2.2 young/nest in 1976 (N = 25) and 2.5 young/nest in 1977 (N = 28). Predation on and starvation of nestlings were the primary reasons for the low productivity/clutch-size ratio. Renesting after egg destruction was observed on seven occasions with renesting after predation of hatchlings observed four times in the study. Productivity and renesting after hatchling destruction have not been reported previously in natural populations of Common Ravens.

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